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Irrigation and elevated carbon dioxide effects on whole canopy photosynthesis and water use efficiency in cotton (Gossypium hirsutum L.)

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Abstract

The study compared the effects of water stress under ambient (350 μ mol mol⁻¹) and elevated (700 μ mol mol⁻¹) carbon dioxide concentrations on canopy carbon assimilation rates, soil water use, and water use efficiency (WUE) of cotton plants on a daily basis. This research was carried out in four sun-lit SPAR (Soil Plant Atmosphere Research) units with soil bins located at Beltsville, Maryland, USA. Whole canopy net photosynthetic rates were recorded at 5-min intervals, and soil water content was measured hourly using time-domain reflectometry. Pre-dawn and mid-day leaf water potentials were measured during the water stress and the recovery periods. The soil water use rates of plants grown under elevated CO_2 were significantly lower than those grown under ambient levels for both water-stressed and well-watered plants. The WUE of the ambient treatment did not begin to increase until most of the available water was depleted from the soil. The elevated CO_2 non-irrigated treatment was able to maintain carbon assimilation rates similar to that of the well-watered treatment while decreasing water uptake during the first 10 days of the drying period. Both water use and carbon assimilation rates decreased in the ambient non-irrigated treatment, shortly after withholding water. Plants grown at 350 μ mol mol⁻¹ CO_2 concentration depleted more water from the deepest part of the profile (0.35–0.85 m) than did the plants from the elevated CO_2 treatment.

Keywords: Canopy photosynthesis, TDR, water deficit, water uptake

Introduction

The carbon dioxide (CO₂) of the atmosphere is increasing and is expected to double sometime near the middle of this century (IPCC 2001). As a result, crops will likely grow under higher levels of atmospheric CO₂ in the future. In experiments using elevated CO₂, carbon assimilation rates for C₃ plants have been reported to be 25–50% higher than rates under ambient CO₂ (Baker 2004; Wu et al. 2004; Finnan et al. 2005). As a result, elevated CO₂ has a fertilization effect on many crops and results in higher biomass and seed or fruit yields. At elevated CO₂, stomatal conductance is often reduced compared with ambient CO₂ treatments (Morison 1998; Bunce 2000) resulting in lower transpiration rates than in plants grown at ambient CO₂ levels. In fact, some increase in

biomass or yield at elevated CO_2 have been attributed to increased water use efficiency (WUE, g dm 1^{-1} H_20) (Soinit et al. 1980; Ownesby et al. 1993; Remy 2007).

The increased WUE is due to the increased efficiency of carbon assimilation and related reduction in stomatal conductance at elevated CO_2 . The effects of water stress on carbon assimilation can often be alleviated by increasing the CO_2 around the leaf (Lawlor 2002). The reduction in transpiration rate also leads to higher water contents in the soil compared to plants grown under ambient CO_2 levels. In a study on barley in pots, Robredo et al. (2007) reported that after a 16-day drying period, soil water content was reduced 88% under ambient CO_2 but only 75% under elevated CO_2 (700 μ mol 1^{-1}). A reduction in transpiration rate of about 10%

has been reported for soybean canopies grown at $660 \mu \text{mol}$ $\text{CO}_2 \text{ mol}^{-1}$ over the growing season (Jones et al. 1985) and for rice (Baker et al. 1997). Non-irrigated peanut under elevated CO_2 in a greenhouse extracted much less water by the end of the growing season than plants grown at ambient CO_2 (Clifford et al. 1995). Wall et al. (2001) also reported higher soil water contents under elevated CO_2 in sorghum in FACE (free air carbon dioxide enrichment) experiments under field conditions. Baker et al. (1997) reported similar results for rice grown in growth chambers with soil bins.

The effects of elevated CO₂ on stomatal conductance and water efficiency have important implications for plant responses to decreasing soil water content, especially plant water status. Many plants, such as cotton undergo decreased tissue water potential in response to increased resistance to water flow as the soil dries (Ephrath & Marani 1993; Ephrath et al. 1993). In peanut (Clifford et al. 1993), barley (Robredo et al. 2007) and sorghum (Wall et al. 2001) higher mid-day leaf water potential (LWP) were recorded under well-watered conditions for plants grown at elevated CO₂ compared to plants grown at ambient CO₂. Under water stress conditions, the mid-day LWP of plants grown under elevated CO₂ were also higher than those grown under ambient CO₂.

Increased WUE under elevated CO2 extends to conditions where water is limited and can result in increased available water and maintenance of growth rate. Kang et al. (2002) studied water uptake in maize, cotton, and wheat. They reported that transpiration rate under water stress was greater for plants grown under elevated CO2 than for plants grown at ambient CO₂. This was at least partially due to the initial lower water uptake rates in elevated CO₂ plants that resulted in conservation of soil water and an extension of time until drought effects were experienced. Baker et al. (1997) showed that, for rice, CO₂ enrichment allowed 1-2 days of additional available water before water stress effects were seen. Robredo et al. (2007) reported that after withholding water for 9 and 13 days from potted barley plants, the LWP of the plants grown at elevated CO₂ at 13 days were still larger than those of the ambient grown plants after 9 days of withholding water. This effect can be partially offset however by the more rapid increase in leaf area index in CO2 enriched plants that can result in more rapid removal of water from soil (Jones et al. 1985). Root growth has also been shown to be stimulated in FACE experiments under elevated CO₂ (Kimball et al. 2002). This may enhance the plant's ability to transpire water under water limiting conditions. In a review of crop response to CO₂, Kimball et al. (2002), the authors, noted that in general, for C₃ plants, there was a greater response (increased yield and growth) to

elevated CO₂ under water stress than under well-watered conditions.

Plant water uptake has been measured in FACE experiments that have allowed the use of natural soil environments (Conley et al. 2001; Hunsaker et al. 2000). These studies have quantified water content for a profile to estimate evapotranspiration. A crop coefficient is used to distinguish soil evaporation from plant transpiration (Hunsaker et al. 2002) or they were lumped together as evapotranspiration (Conley et al. 2001). These studies have provided useful information on trends in water uptake as a function of CO_2 enrichment but there is little detailed temporal and spatial (depth) information on water uptake.

Many of the studies on transpiration and photosynthetic rate in plants grown under water stress and elevated CO₂ have been carried out in pots or small containers. The field level studies on water uptake generally reported infrequent or end of season water content measurements. Furthermore, these studies have reported leaf level photosynthetic rates for specific periods. Data on whole canopy photosynthesis and water uptake at similar temporal scales could provide a better insight into plant responses to elevated CO2 under water stress. The higher LWP and lower stomatal conductance of plants grown under elevated CO2 may also be related to limited root activity (i.e. water uptake) in deep soil layers but there is little research in this area. The objective of this study was to investigate water uptake and canopy level photosynthesis of cotton plants grown under ambient (350 μ mol mol⁻¹) and elevated (700 μ mol mol⁻¹) CO₂ in large root volumes and subjected to water stress at full canopy development. The hypothesis that plants grown under ambient CO2 will obtain a larger fraction of water from soil depths greater than 30 cm than will plants grown under elevated CO₂ was tested.

Materials and methods

Cotton (Gossypium hirsutum L, cv Acala, DP 0924 B2RF) was planted on 8 May 2001 in four outdoor, sunlit, controlled-environment Soil Plant Atmosphere Research (SPAR) chambers (Pickering et al. 1994; Tingey et al. 1996; Reddy et al. 2001). The SPAR chambers consist of transparent chamber tops, 2.2 m × 1.4 m × 2.5 m (length × width × height) constructed of 0.0127 m thick Plexiglas. Each SPAR chamber top is mounted to a steel soil bin measuring 2.0 m × 0.5 m × 1.0 m (length × width × depth). A physical description of these SPAR chambers and methods of operation and monitoring have been described previously (Baker et al. 2004). In a study using wheat, Fleisher et al. (2009) showed that the environmental conditions

(temperature, CO₂) inside the SPAR chambers are controlled well. The variation in measured plant biomass, carbon assimilation and development stage was not significantly different among chambers when the same crop (wheat) and management were used for all chambers. Furthermore, it was shown that the variation of measured plant data (biomass, canopy carbon assimilation, development stage, etc) within chambers was generally higher than the variation of these plant data between chambers. The within chamber variance was likely due to variable light conditions inside the chambers (Kim et al. 2004).

The soil bins were filled in layers (approx 0.15 m thick and 2×0.50 m in area) and wet thoroughly as each layer was added. The soil type consisted of 66% sand and 33% vermiculite (Grace Construction Products, USA.) by volume. The day/night temperatures were set at 30/20°C. After the cotton plants had emerged, they were thinned to 25 plants per chamber (m⁻²). The chambers were initially fertilized with 0.250 kg of a 20-20-20 mixture of N-P-K mixed with water and then bi-weekly with 0.015-0.060 kg of the same fertilizer. The plants were planted in five rows, 0.40 m apart, with five plants in each row (0.10 m between plants within the row) in each growth chamber (25 plants per chamber (m⁻²)). Irrigations were provided by compensated drippers arranged in three 2.0 m rows with an approximate spacing between rows of 0.20 m. The drippers were approximately spaced at 0.10 m intervals. The drip irrigation system supplied approximately 80 + 3 liters per hour of water.

Plants in two chambers were grown under elevated (700 μ mol mol⁻¹) and in the other two units at ambient (350 μ mol mol⁻¹) CO₂. These values were chosen because it is expected that CO₂ concentration will reach levels of 600–1000 μ mol mol⁻¹ CO₂ by the end of this century (Cox et al. 2000). Several studies examine different responses of cotton to similar CO₂ concentrations (Yoon et al. 2009). Increasing CO₂ from 360 μ mol mol⁻¹ to about 750 increases the yield by 40–50% (Kimball & Mauney 1993; Reddy et al. 2000).

One chamber in each CO₂ group was chosen as irrigated control. The remaining chamber in each CO₂ group was designated as non-irrigated chamber. The treatment codes are EI and EN for elevated CO₂ (E) irrigated (I) and non-irrigated (N), respectively and AI and AN for the ambient treatments (A). Before imposing water stress, during the early growth period, the soil in the SPAR units was irrigated four times a week. Beginning from 3rd July 2000, 52 days after emergence (DAE), the non-irrigated chambers (EN and AN treatments) were subjected to water stress conditions by withholding irrigation. The control chambers (EI and AI treatments) were irrigated daily with about 12–20 mm of water. This

amount was enough to replace water used the day before, but not enough to saturate the soil, which would have resulted in drainage from the soil bin. Irrigation was resumed after about 3 weeks in all chambers on 25th July, 74 DAE. The plants were harvested on 8th August, 92 DAE. None of the chambers were fertilized from 3rd July to 25th July, the end of the drying period. The soil was covered with plastic in all chambers on 18th July, 12 days after the irrigation treatments were imposed in order to exclude soil and root respiration from measurements of CER. CO2 leakage rates were measured using mean resistance values from CO2 drawdown tests on empty chambers (Acock & Acock 1989) after the experiments were finished (repeated three times). The resistance value from CO₂ drawdown tests on an empty chamber represents a one-time value from a time-point after the experiment is finished. The resistance was calculated from:

$$L = \frac{1}{r} (\Delta CO_2) \tag{1}$$

where L is the leakage rate (μ mol CO₂ m⁻² s⁻¹), e.g. the CER (Carbon Exchange Rate) without plant uptake, and Δ CO₂ is the gradient of internal and external CO₂ concentrations (μ mol CO₂ mol air⁻¹). The value of the resistance, r, is obtained by regressing CER on the CO₂ gradient (Δ CO₂). The relationship was strongly linear for all data sets.

When plants are growing in the chamber, the CER represents net photosynthesis (P_N) and is adjusted for respiration to obtain gross photosynthesis, P_G . Respiration was calculated daily as the mean CER between the hours of 1 and 4 am before there is any significant light. Gross photosynthesis (P_G) was therefore calculated as:

$$P_G = P_N + R_D \tag{2}$$

where P_N is the CER measured during daylight hours, and R_D is dark respiration ($R_D > 0$). All units are μ mol CO_2 m⁻² s⁻¹. The use of R_D to adjust photosynthesis has been shown to provide estimates of seasonal carbon assimilation that agree closely with measured plant biomass (Reddy et al. 1989; van Iersel & Kang 2002). Respiration calculated from night-time CER was adjusted for daytime temperatures using relationships from Reddy et al. (1991). As crop canopy had closed in all chambers before the irrigation treatments were imposed, P_G should not have to be adjusted for light interception.

Soil water content was measured hourly at five depths (0.10, 0.25, 0.40, 0.55, and 0.75 m), replicated three times per depth (60 locations for four chambers), using Time Domain Reflectometry (TDR) (Topp et al. 1980; Timlin et al. 2007).

Tektronix 1502 cable testers (Tektronix, Beaverton, OR) were connected to the probes through Campbell Scientific SDMX50 coaxial multiplexers (Campbell Scientific, Logan, Utah). Two cable testers were used, each one monitoring 45 probes. The data acquisition was controlled by a program called TACQ (Evett 1998, Evett 2000) running on each of two IBM-PC computers (one for each cable tester). The program also interpreted the wave forms and calculated the apparent dielectric constant from the recorded waves. A calibration relationship between water content and dielectric constant was developed using soil from the chambers. Water contents from air dry to saturation were used. The hourly water contents were multiplied by soil volume for each layer to obtain total volume of water in the soil bin for each hourly measurement (Timlin et al. 2007). The hourly water volumes were averaged by depth and summed to obtain a daily total water volume in the soil bins. Water use per day was obtained from the difference between the 8 am and the 10 pm water contents to minimize the effect of night-time irrigation on water content.

Plant heights and numbers of main stem nodes were measured bi-weekly. LWPs (Scholandar et al. 1965) were measured at pre-dawn (6 am) and midday (12 noon) respectively on selected days using a pressure chamber (Soil Moisture Corp, Santa Barbara, CA) during the period that the plants were subjected to water stress and during the recovery period. Four leaves from each treatment were clipped and immediately placed on a wet paper towel in a plastic bag in an ice-filled box. Measurements were taken within 10 min of leaf selection. At the end of the season, the plants were removed from the chambers and weighed individually for stem, leaf, boll, and flower weights, and the number of nodes, bolls, and flowers were also counted. Leaf area measurements were made using an automatic area meter (Hayshi Dewnko Co., Tokyo, Japan). The plant parts were dried at 75°C for 5 days. In addition, the soil was dug from the soil bins and eight soil cores measuring 0.102-m diameter × 0.15-m long were collected every 0.15 m from the surface to the bottom of the soil bin. The soil was washed from the cores and the fine roots were saved for further analysis.

The washed roots, from 15 soil cores, were spread on a water film and photographed using a digital camera. There was a high-linear correlation $(R^2 = 0.83)$ between root dry weight and root length density (RLD), defined as the ratio between root length and soil volume (cm cm⁻³). This regression equation was used to estimate the RLD of all the soil core samples, which were taken at the end of the growing season. These data were used to determine the relationship between total above ground dry weight and RLD.

Canopy photosynthesis model

The response of gross photosynthetic rate (P_G) to light intensity (photosynthetic photon flux density (PPFD)) was fitted by means of an exponential rise to a maximum function (P_{MAX}) of similar form to that of Constable and Rawson (1980) and Milroy and Bange (2003). This equation was used to interpolate measurements of P_G for periods, when gas exchange data were missing or out of range as when the chambers were opened for plant measurements, smooth the data and obtain P_G values for specific light levels:

$$P_{G} = P_{MAX}(1 - \exp\left[-a \times I\right]) \tag{3}$$

where I is light intensity (PPFD, μ moles Quanta (Q) m $^{-2}$ s $^{-1}$); P_{MAX} is the asymptotic rate of gross carbon assimilation (μ mol CO_2 m $^{-2}$ s $^{-1}$) at light saturation, a is a coefficient with units of μ mol photons⁻¹ m² s. P_G, gross carbon assimilation rate, is calculated as net carbon assimilation rate measured in the chambers with respiration added back as a positive number ((Equation (2)). Unless noted in the article, P_G is reported as gross carbon assimilation per unit surface area of the growth chamber and is not adjusted for light interception or leaf area. Proc NLIN of SAS (SAS Institute, Inc. 1999) was used to fit the parameters (a and P_{MAX}). Values at a light level of 1600 μ moles Q m⁻² s⁻¹ were predicted for each curve and the standard deviation of the interpolated value was also recorded as an estimate of the error.

Statistical analysis

Statistical analysis was carried out on the harvest data using Proc GLM provided by the SAS Institute (SAS version 8, SAS Institute, Inc. 1999). As there were multiple plants within a chamber, the variance in plant biomass measurements was a pseudo variance. Treatment differences were tested using least square means (LSMEANS, keyword in SAS). In order to compare the treatment effects on photosynthesis, daily cumulative carbon assimilation was calculated using measured light data and carbon assimilation rates were calculated using Equations (2) and (3). These daily amounts of assimilation were summed to determine the cumulative carbon assimilation over the treatment period. The slopes (cumulative carbon assimilation vs. time) of these were compared using Proc Mixed in SAS (Littell 1996; SAS version 8, SAS Institute, Inc. 1999). When calculating the slopes of the regression curves, chambers were treated as experimental units with chamber as a repeated measure. A first-order autoregressive process was used to model the covariance over time, where applicable. Individual intercepts and slopes were calculated. Within chamber variance of water content, measurements were obtained from the three replicate wave guides installed at each depth.

Results

SPAR environment

Temperatures in the SPAR units were maintained within 1°C of the day/night setpoints of 30 and 20°C, respectively (Table I). CO2 control was, on the average, within 22 μ mol mol⁻¹ of the setpoint (Table I). The difference was usually within 2-3 μ mol mol⁻¹ when the chamber doors were kept closed. Opening the chamber doors for measurements results in loss of control, and CO2 levels will fall or climb depending on the difference between the outdoor ambient CO2 level and the control level in the chamber. The chambers were not opened for measurements every day and when opened, only for periods less than 1 h. Night-time values of average CO2 levels are not given as there was no control of CO₂ at night. Even with these perturbations, CO₂ concentrations were close to the setpoint values. Dew point temperatures, a function of relative humidity, were within 2-3°C of each other (Table I). This is an average over the growing period; the differences were larger depending on how much water the plants were transpiring during the water stress period.

Soil water uptake

The daily water uptake rates for the elevated CO_2 treatments were less than the water uptake rates for the ambient treatments before the water stress treatments were imposed (Table II). There were

small non significant differences in water uptake rates within a CO2 treatment before water stress was applied. Cumulative water uptake was 18.6 cm cm^{-2} (186 l) for the EI treatment and 29.1 cm ${\rm cm}^{-2}$ (291 l) for the AI treatment (Figure 1). The daily water uptake rate in the EI treatment doubled more than by the end of the water stress period (Table II). In the AI treatment, there was only about a 50% increase in daily water uptake. In the EN treatment, there was a small increase in daily water uptake by the end of the drying period. A sharp decrease in daily water uptake occurred in the AN treatment (Table II). The mean cumulative water uptake for the EN treatment was less than cumulative water uptake for the AN treatment (approx 12.5 cm cm $^{-2}$ (125 l) vs. 18.0 cm cm^{-2} (180 l)), (Figure 1). The cumulative water uptake was less for the non-irrigated than for the irrigated within a CO₂ treatment.

The dynamics for the changes in the amount of water in the soil profile (Figure 2) were different between the two non-irrigated treatments. In the upper profile (Figure 2a), there was no discernable difference between the AN and EN treatments. From 0.15 m down to the bottom of the soil profile (Figure 2b-2e), the differences between the nonirrigated treatments increased. The AN treatment depleted more water than the EN treatment did, especially in the deeper parts of the profile. The available water in the AN treatment is largely depleted by the end of the treatment period (based on the low-water content and lack of changes). Available water still remained in the soil for the EN treatment. The available water appeared to have been completely depleted in the AN treatment, about 20 days after withholding irrigation. Only small differences were noted for the irrigated treatments except at the deepest layer (Figure 2e), where there was less water in the soil with the EI treatment. This is

Table I. Statistics for temperature, CO₂, and humidity control in the growth chambers.

Treatment	Period	Mean daily difference between measured temperature and setpoint temperature (°C)	Standard error of difference (°C)	Mean daily difference between measured CO_2 concentration and CO_2 setpoint (μ mol m ⁻² s ⁻¹)	Standard error of difference (μ mol m ⁻² s ⁻¹)	Mean daily dew point temperature (°C)	Standard error of dew point temperature (°C)
EI	Day	-0.83	0.02	-19.46	3.92	22.05	0.33
EI	Night	-0.05	0.10	-1	_	20.55	0.14
EN	Day	-0.17	0.01	-16.79	3.70	23.76	0.26
EN	Night	0.45	0.09	_	_	20.51	0.13
AI	Day	-0.92	0.02	16.12	1.38	26.09	0.38
AI	Night	-0.06	0.09	_	_	23.22	0.20
AN	Day	-0.78	0.01	15.84	1.26	24.35	0.16
AN	Night	-0.05	0.10	_	_	20.25	0.17

Note: ¹CO₂ was not controlled at night.

The day and night periods had different setpoint temperatures.

Table II. Average daily water uptake (mm d^{-1}) during the beginning and the end of the drying period.

		Period					
	(4th Jul	DAE 53–59 (4th July–10th July)		0–74 July– July)			
	Mean	SE ¹	Mean	SE			
	mm	mm d ⁻¹		${ m mm}~{ m d}^{-1}$			
CO ₂							
Elevated							
Irrigated (EI)	4.8	0.8	11.0	0.8			
Non-irrigated (EN)	4.3	0.9	5.8	0.2			
Ambient							
Irrigated (AI)	8.5	1.6	12.5	1.0			
Non-irrigated (AN)	7.0	1.0	2.5	0.3			

Note: ¹Standard error of the mean based on three replicate water contents at each depth and the 7-day measurement period.

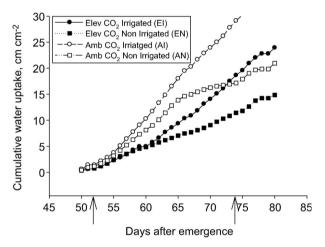


Figure 1. Cumulative water uptake from 3 days before initiation of the treatments to 10 days after resumption of irrigation. The vertical arrows along the *x*-axis indicated the start and end of the dry-down period.

possibly because of the lower irrigation rate for the EI treatment that did not replenish all the water in the 0.65–0.85-m deep layer. Root activity for the irrigated treatments, as evidenced by water use rates (Figure 3), was largely confined to the surface (25 cm). Root activity for the EN treatment lagged behind that of the AN treatment by about 10 days at depths greater than 0.40 m. The high water use rate in the 0.40–0.55 m layer from DAE 60 for the AN treatment is shown in Figure 3. A similar increase in water use occurred for the EN treatment after DAE 67 at 0.40 m and DAE 72 at 0.55 m. The rates decreased because of water depletion (Figure 2).

Leaf water potentials

LWP was affected by the CO₂ and irrigation treatments (Figure 4). The pre-dawn LWP for the irrigated treatments were generally similar and higher than the non-irrigated treatments. At 72 DAE, 20 days after withholding irrigation, the EN treatment had a significantly higher pre-dawn LWP compared to the AN treatment. The pre-dawn LWPs of the non-irrigated treatments were significantly lower when compared with the irrigated treatments from 65 DAE, both under the elevated and ambient CO₂.

From 55 to 67 DAE (3 to 15 days after withholding water), mid-day LWP fluctuated somewhat but there were not consistent differences among the mid-day LWPs of the various treatments (Figure 4). After 67 DAE, significant differences both between and within the CO₂ and the irrigation treatments were recorded. The LWP of the EI treatment was the highest, followed by the AI and the EN. The non-irrigated treatments developed lower mid-day LWP (Figure 4). The differences in the LWP between CO₂ levels for the non-irrigated treatments were larger toward middle and end of the drying period when available water was largely depleted in the AN treatment.

The AN treatment had a longer recovery time after resuming irrigation when compared with the EN treatment. Five days after resuming irrigation, the LWP for the EN treatment was higher than the LWP of the AI treatment. The AN treatment developed significantly lower mid-day LWP than the EN treatment.

Whole canopy gas exchange rates

Diurnal gross photosynthetic rates (P_G) and PPFD averaged over 15-min periods are shown for two representative days (Figure 5a and 5b). The data in these figures represent periods of 4 days before irrigation was withheld (51 DAE, Figure 5a) and 1 day before resuming irrigation (74 DAE, Figure 5b). Initially, there was small variation in P_G within a CO₂ treatment. At the end of the water stress treatment period (74 DAE), there were large differences in P_G rates compared with irrigated for non-irrigated treatments in each of the CO₂ treatments (Figure 5b). The difference in P_G within a CO₂ treatment was larger for ambient conditions compared to elevated.

Cumulative carbon assimilation increased steadily with time in the irrigated treatments (Figure 6). The slopes, which represent daily gross carbon assimilation rates, are smaller for the non-irrigated treatment than for the irrigated treatment at the same CO₂ level (Table III). The total cumulative gross photosynthesis for the EN treatment was higher than for the AI

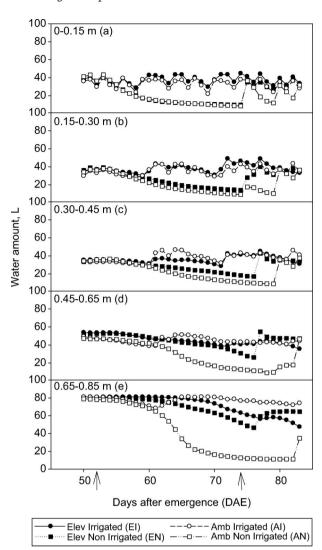


Figure 2. Temporal changes in soil water contents in the soil bins. (a) 0-0.15 m; (b) 0.15-0.30 m; (c) 0.30-0.45 m; (d) 0.45-0.65 m; (e) 0.65-0.85 m. The vertical arrows along the *x*-axis indicated the start and end of the dry-down period.

treatment in spite of reduced irrigation. The slopes of cumulative carbon assimilation over the drying period (DAE 53–74) show significant irrigation effects within a CO_2 treatment (Table III). There was a 19% decrease in cumulative carbon assimilation over the 20-day drying period because of water stress for the ambient CO_2 treatment and a 14% decrease for the elevated.

Plant growth

Full light interception based on plant height and row spacing occurred at about 59 DAE (10th July) for all treatments, although plant height continued to increase (Figure 7). The plants in the AN treatment were the first to show effects of water stress on plant height, beginning about 70 DAE (Figure 7). The EN treatment had lower growth rates (inferred from

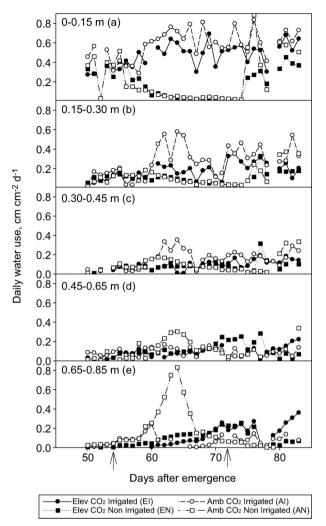


Figure 3. Daily water use as a function of time and soil depth. (a) 0-0.15 m; (b) 0.15-0.30 m; (c) 0.30-0.45 m; (d) 0.45-0.65 m; (e) 0.65-0.85 m. The vertical arrows along the *x*-axis indicated the start and end of the dry-down period.

changes in plant height) than the EI treatment did. There was also no evidence of a precipitous drop in growth rates of the EN treatments as was seen in the AN treatment. The plant heights were similar for the irrigated treatments. The differences in height between the irrigated and non-irrigated treatments were larger than the difference between the irrigated treatments. At the end of the growing season, the plants that grew under water stress conditions and elevated CO₂ were significantly taller when compared with the water-stressed plants grown under ambient CO₂ (Table IV).

Statistics for the final harvest data show that there was a significant irrigation effect for dry matter and leaf area (Table IV). The values of height, total dry weight, and leaf area for the irrigated treatments were significantly higher than for the non-irrigated. There was also a significant interaction between CO₂ and irrigation for height, where the decrease in height

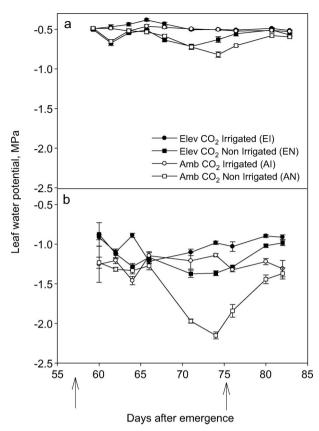


Figure 4. Leaf water potentials during the drying period. Error bars show the standard deviation of the three values used in the measurement. The vertical arrows along the *x*-axis indicated the start and end of the dry-down period.

caused by lack of irrigation was much greater for the ambient CO₂ treatment than for the elevated treatments. This effect was not evident for the other variables, total dry weight and leaf area. Mean root length and root weight showed an irrigation effect only for the elevated CO₂ treatment where they were significantly higher for the EI treatment. This is consistent with other research in growth chambers and rhizotrons. Ball et al. (1994) reported that leaf expansion in cotton was much more sensitive to water stress than root elongation.

There were significant differences for the RLD at the surface (0–0.15 cm) and bottom layers (0.75–0.90 m) (Table V). The root weight in the EI treatment was significantly higher than in the AI treatment. The root weight from 0.55 to 0.75 m (bottom of the soil bin) in the AI treatment was significantly higher than for the AN treatment. There were no significant differences in root density among any of the treatments for layers between the bottom and the surface (Table V).

WUE (moles of CO₂ assimilated per kg of water transpired per day per m²) was strongly affected by both CO₂ and water stress (Figure 8). WUE was higher under elevated CO₂ than under ambient.

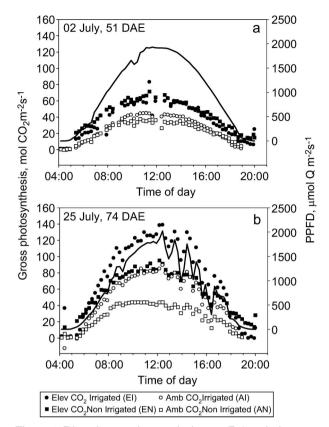


Figure 5. Diurnal gross photosynthetic rate (P_G) and photosynthetic photon flux density (PPFD) for (a) 51 DAE (2 July), 2 days before the last day of full irrigation and (b) 74 DAE (25 July), 1 day before resumption of irrigation. Solid line is PPFD.

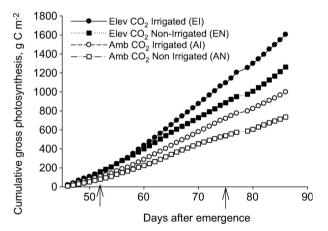


Figure 6. Cumulative daily gross photosynthesis, P_{G} , from 3 days before initiation of the treatments to 12 days after resumption of irrigation. The vertical arrows along the *x*-axis indicated the start and end of the dry-down period. The gap at day 79 was caused by a loss of data due to an electrical failure.

There was also an increase in WUE in the non-irrigated plots beginning several days after irrigation was withheld. Interestingly, the WUE for the EN treatment began to increase before WUE for the AN treatment. The WUE values for the EN treatment, at their maximum difference (between DAE 60 and

Table III. Slopes and intercepts for cumulative gross photosynthesis over the drying period (Figure 7).

	Source						
	Ambient			Elevated			
Type	Irrigated	Non-irrigated	Difference ²	Irrigated	Non-irrigated	Difference ²	
Slope (mol CO ₂ m ⁻² d ⁻¹)	2.2	1.7	0.54**	3.2	2.4	0.94**	
SE ¹ of Slope slope (or difference) (mol CO ₂ m ⁻² d ⁻¹)	0.05	0.05	0.04	0.05	0.05	0.05	
Intercept (mol CO ₂ m ⁻²)	2.7	2.9	-0.20	3.1	6.1	−3.0 *	
SE ¹ of Intercept intercept (mol CO ₂ m ⁻²)	0.76	0.76	1.08	0.76	0.76	1.08	

Note: The difference column shows irrigation treatment effects on cumulative gross photosynthesis.

^{*}Significant at p < 0.05.

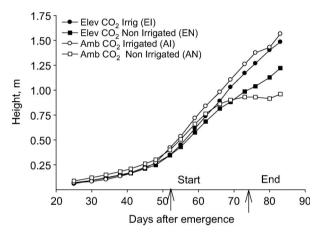


Figure 7. Plant height as a function of time. The vertical arrows along the x-axis indicated the start and end of the dry-down period.

70), were about 400% higher than for the AN treatment. WUE for the AN treatment was not different from that of the AI treatment until most of the available water was depleted (DAE 65). The WUE values for the AN treatment were the highest as the soil water was completely depleted toward the end of the water stress period and were about four times higher.

Discussion

Under conditions of ambient CO₂ and adequate water and nutrients, photosynthetic rates in C_3 plants are usually limited by CO2 concentration (Bowes 1991; Woodward et al. 1991). CO₂ enrichment usually leads to increase in the photosynthetic rates of single, sunlit leaves (Allen et al. 1994; Bowes 1991). When plants are small, the majority of leaves are sunlit, but as plants develop, the percentage of shaded leaves increases, and the net carbon balance of upper, sunlit leaves may become less representa-

tive of the carbon balance of the whole plant canopy. Therefore, plant growth and yield may be more strongly associated with whole plant canopy photosynthesis than with the photosynthetic rates of single leaves (Drake & Leadley 1991).

Overall, we found, in our study, that the elevated CO₂ treatments used less water than the ambient treatments in both well-watered and water-stressed conditions (Figures 1 and 2). van Vuuren et al. (1997) showed that for potted wheat growth chambers, plants grown under ambient CO2 levels used about 1.25 times as much water as plants grown at the elevated CO₂ level for both irrigation treatments. The authors also noted that the soil remained noticeably wetter between irrigations in the elevated CO₂ treatment compared to the ambient. Elevated CO₂ apparently provided about 4 to 5 days of extra water availability in this study. Similar results have been reported in other elevated CO₂ studies (Idso & Idso 1994; Jackson et al. 1994). Baker et al. (1997), using tensiometers to quantify soil water potential in rice, noted that the elevated CO₂ treatment lagged behind the ambient treatment by about 2 days.

The data in Figure 3 indicate that water uptake was shifting to deeper soil layers in the non-irrigated treatments toward new sources of water as water was depleted from surface layers. This shift was earlier for the ambient CO₂ treatment than for the elevated one. In sandy soils, as was used in this study, water movement to the roots will be negligible (Brakke et al. 2003) and therefore, it was likely that there was new root growth into the deeper soil layers for the non-irrigated treatments. The root density data (Table V), however, do not indicate greater end of season root densities in the AN treatment over the AI treatment in the deeper soil layers. In fact, the root density for the AI treatment was higher in the 0.76 to 0.90 m layer than that of the AN treatment. This may be due to root death in the lower layers in the AI treatment because the root density was measured

¹Denotes standard error of the estimate.

²Difference between the slopes for irrigated and non-irrigated treatments.

^{**}Significant at p < 0.01.

Table IV. End of season height, dry matter, and leaf area per plant.

	CO_2	Non-irrigated			Irrigated			
Variable		Mean		SD	Mean		SD	
Root weight (g)								
Ambient		5.0	a^1A^2	0.97	4.7	aA	1.27	
Elevated		3.6	aA	0.59	6.4	bB	1.09	
Root length (m)								
Ambient		55.96	aA	6.32	53.31	aA	8.48	
Elevated		47.68	aA	3.88	66.57	bB	7.24	
Leaf area (m ²)								
Ambient		0.2249	aA	0.0190	0.4527	bA	0.0427	
Elevated		0.3491	aB	0.0408	0.4725	bA	0.0501	
Above ground bi	omass (g)							
Ambient		29.7	aA	3.0	50.4	bA	6.0	
Elevated		35.6	aB	4.6	56.9	bA	8.4	
Height (m)								
Ambient		0.95	aA	0.028	1.47	bA	0.053	
Elevated		1.29	aB	0.059	1.49	bA	0.064	

Note: ¹Values followed by same lowercase letters in a row indicate no significant differences between irrigation treatments for that CO₂ treatment.

Table V. Root length density as a function of depth and treatment.

	CO ₂	Non-irrigated			Irrigated				
		Mean		SD	Mean		SD		
Depth (m) 0-0.15		$\mathrm{m}~\mathrm{m}^{-3}$							
		1736.48	a^1A^2	213.67	1344.07	aA	269.15		
	Elevated	1424.27	aA	170.51	2475.26	bB	245.60		
0.16-0.30	Ambient	813.56		171.21	824.38		192.57		
	Elevated	685.16		67.47	842.68		125.43		
0.31 - 0.45	Ambient	599.47		54.56	535.41		41.27		
	Elevated	508.23		36.24	631.92		105.16		
0.46-0.60	Ambient	623.32	A	54.17	586.44		39.69		
	Elevated	454.99	В	29.10	496.03		15.09		
0.61-0.75	Ambient	566.75		26.66	555.10		27.18		
	Elevated	522.93		9.36	627.48		61.31		
0.76-0.90	Ambient	391.76	a	14.32	661.59	b	147.05		
	Elevated	435.85		15.86	555.66		59.31		

Note: ¹Values followed by same lowercase letters in a row indicate significant differences between irrigation treatments for that CO₂ treatment.

toward the end of the season, after re-watering. Recovery of root growth beginning in the surface layers first may also be the reason for the higher root density in the surface soil for the AN treatment compared to the AI (Table V).

The LWP data (Figure 4) are consistent with the differences in water uptake among the treatments. Wall (2001) reported similar results for wheat grown under ambient and elevated CO₂ in the field. On the other hand, elevated CO₂ has also been shown to have had little effect on LWP under water-stressed conditions in cotton (Bhattacharya et al. 1994). This

result may have been due to low levels of water stress since the authors only saw water stress effects on LWP at the end of the growing season. From a hydraulic perspective, LWP has been shown to be the driving force to overcome resistances in the plant and soil transport stream as water moves from the soil, through the roots and plant vascular system and out through the leaves into the atmosphere. Reicosky and Ritchie (1976) showed that LWP was proportional to the total soil and plant resistance. A main component of plant resistance is root resistance (Reicosky & Ritchie 1976). Root resistance is less for

²Values followed by same uppercase letters within a column indicate no significant difference between CO₂ treatments for that irrigation treatment.

²Values followed by same uppercase letters within a column indicate significant difference between CO₂ treatments for that irrigation treatment.

shallow root systems (given a shorter path for water to travel in the root system). Therefore, LWP would be expected to be high under conditions of water uptake from shallow depths and high water contents, conditions associated with elevated CO₂ in this study. As the water uptake moved to deeper layers and the soil dried in the AN treatment, the LWP decreased (became more negative). From a hydraulic standpoint, the decrease in LWP would result in an increasing gradient in water potential between the plant transpiring surface and soil that would allow transpiration fluxes to continue at the same rate similar to the earlier growth period but over a longer root path.

There was greater water uptake from the deeper soil layers by the plants in the ambient CO₂ treatments than in the elevated treatments (as inferred from water contents in Figures 2 and 3) even though end of season root densities were not that much different in the deeper layers among the CO₂ treatments (Tables IV and V). Van Vuuren et al. (1997) noted that reduced water uptake and an increase in soil wetness under elevated CO₂ may have implications for nutrient uptake. However, the greater amount of root density found under elevated CO₂ may have been able to compensate for loss of nutrients in mass flow of water into the plant by allowing an increase in diffusive flow of nutrients.

Despite large differences in water uptake between the irrigated and non-irrigated treatments, there were smaller differences in PG. Total water uptake decreased by 39% for the ambient CO2 and 34% for the elevated CO2 treatment when irrigation was withheld. Cumulative carbon assimilation, however, was reduced by a smaller amount, 19% in the ambient treatment and 14% in the elevated CO₂ treatment. An increase in WUE has been observed in other irrigations (Flènet et al. 1996) and CO₂ studies (Allen et al. 2003) as well. The largest differences in P_G between irrigated and non-irrigated treatments were at high light levels (Figure 5). Similar differences in canopy P_G under irrigated and non-irrigated conditions have also been observed in soybean (Baker et al. 1997). WUE increases with CO₂ amendments. Wu et al. (2004) and Remy et al. (2007) reported that elevated CO₂ greatly increased WUE when compared to WUE under ambient conditions in wheat. Note that PG for the nonirrigated elevated CO₂ treatment was similar to P_G for the irrigated ambient CO2 treatment. This suggests that elevated CO2 compensated for decreased stomatal conductance due to water stress.

The WUE for the non-irrigated treatments increased substantially as the soil water was depleted for both CO₂ treatments (Figure 8). The WUE values for the AN treatment were the highest as the soil water was completely depleted toward the end of

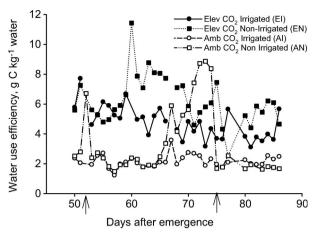


Figure 8. Water use efficiency as grams carbon assimilated (gross) per liter of water taken up. The vertical arrows indicate the start and end of the drying period.

the water stress period and were about four times higher than the irrigated treatment. Because WUE is calculated here as carbon assimilation per unit of water, it will increase if either the amount of water taken up increases or the amount of carbon assimilation decreases. If both carbon assimilation and water uptake decrease at the same rate, then the ratio will remain unchanged. The cumulative carbon assimilation (Figure 6) began to decrease in the EN treatment, relative to the irrigated treatment, at about 60 DAE. Water uptake also decreased as evidenced by the depletion of water in the surface soil layer without a compensatory increase in water uptake from deeper layers (Figures 2 and 3). The relative decrease in water use was greater than the decrease in carbon assimilation resulting in an increase in WUE. There was a trend of decreasing and then increasing WUE for the EN treatment at around 70 DAE. The decrease corresponded with an increase in water uptake from soil depths greater than 0.45 m (Figure 3e and 3f).

In the case of the AN treatment, the increase in water uptake from the deeper layers made up for some of the loss of available water in the surface soil. There was also a decrease in carbon assimilation (Figure 6) for the AN treatment but the water use and carbon assimilation decreased proportionally, resulting in no change in WUE. WUE increased later in the drying period in the AN treatment when the water was close to being depleted (around 70 DAE). This suggests that the regulation of stomatal conductance was able to reduce water uptake without greatly affecting carbon assimilation rates in the EN treatment.

There were significant irrigation effects on plant height (Figure 7), leaf area, and total weight (Table III). The only significant CO₂ effect was on plant height. There were no consistent significant

differences in total RLD among the treatments as a function of soil depth (Table V). The elevated CO₂ treatments, however, did tend to have higher though non-significant root densities than the ambient treatments did. The lack of an irrigation effect on RLD could have been because of additional root growth during the 2-week period following rewatering the soil.

Prior research has suggested that plants grown at elevated CO2 may better compensate for water stress (Rogers et al. 1994; Wechsung et al. 1999) The evidence for this was taken as the increased root growth and higher yields under limited irrigation at elevated CO₂ when compared with ambient CO₂ treatments with the same irrigation level. However, it is difficult to stress (water) elevated CO₂ plants to the same degree as ambient CO2 plants. Because of the lower transpiration rates of the elevated CO₂ plants, the associated soil water contents will generally be higher under elevated CO₂, especially if plants are irrigated as a function of potential evapotranspiration rather than actual water uptake. In this study, plants grown under elevated CO2 and not irrigated (EN) took longer to utilize water from deeper in the soil profile than the plants grown under non-irrigated, ambient CO₂ levels (AN) and this appeared to affect WUE. Carbon assimilation rates did not decrease proportionally with water uptake in the EN treatment and initially remained close to those of the irrigated treatment. As a result, WUE was initially higher in the EN treatment as compared to AN. Plants grown under ambient CO₂, when initially exposed to drying soil, compensated by increasing water uptake from deeper layers and decreasing carbon assimilation relative to the irrigated treatment resulting in no change in WUE.

The plants grown under elevated CO₂ behaved like plants grown under a climatic regime with lowevaporative demand or grown in soils with high water availability, so that soil factors can have a greater effect on plant response compared to the effect of atmospheric factors (Wall 2001). There was more water uptake from deeper layers (> 0.25 m) under ambient CO2 non-irrigated treatments than under elevated ones during the drying phase. Irrespective of CO₂ level, the non-irrigated plants could reduce the water content in the surface layers to similar water contents. The WUE, defined by the daily carbon assimilation rate divided by the daily water uptake rate, was calculated for all treatments. The daily WUE values for the non-irrigated elevated CO₂ treatment increased over that of the irrigated treatment, shortly after irrigation was withheld. The increase was due to a relatively larger reduction in water uptake over carbon assimilation. There was no relative increase in WUE for the ambient treatment until later in the drying phase when most of the water

in the soil was depleted. Carbon assimilation rates decreased 3–4 days after irrigation was withheld, but water uptake from deeper soil layers maintained water availability resulting in no relative change in WUE for the non-irrigated ambient treatment. The maximum relative difference in WUE for the ambient treatment was approximately 400% while that for the elevated CO₂ treatment was approximately 80%.

Plants grown at elevated CO₂ and under soil water regime, which presents only mild or minimal drought stress, will, probably, have no significant root activity to the same depth as plants grown under ambient CO₂ levels for the same soil water regime when the potential evapotranspiration rates are similar. This has implications for nutrient use from deep layers in the soil. Wheat is grown, for example, to scavenge nitrogen from a previous vegetable or legume crop (Gan et al. 2003). If the nitrogen moves too deep into the soil it may not be available for use in an elevated CO₂ climate. Furthermore, the nitrogen left in the soil has the potential to move to ground-water if not taken up. Crop models that simulate responses to elevated CO₂ must also simulate water uptake as function of depth. Although this may not have an impact on yield in an environment with sufficient available water, there may be large differences with respect to nutrient availability, especially from deeper in the profile.

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